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Phylogeny of the Hylocomiaceae (Mosses, Order Hypnales) Inferred from Ontogenetic and Morphological Characteristics

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ABSTRACT: The phylogeny of Hylocomiaceae is inferred by cladistic analyses of twenty-nine morphological characters and the ontogenetic sequences of paraphyllia, central strands, and axillary hairs. The entire ontogenetic transformations are recognized as characters, and character variation is polarized by outgroup comparisons. Two equally parsimonious trees produced by heuristic searches of PAUP support the monophyly of the Hylocomiaceae, which is closely related to family Hypnaceae, containing eight genera *Hylocomium, Loeskeobryum, Leptocladiella, Hylocomiastrum, Neodolichomitra, Macrothamnium, Leptohymenium,* and *Orontobryum*. Hylocomiaceae is diagnosable by sympodial growth-form, excepting *Orontobryum*. The genera *Rhytidium, Rhytidiadelphus, Pleurozium,* and *Rhytidioposis* are excluded from the Hylocomiaceae and comprise a monophyletic family, Rhytidiaceae. Based on the reconstructed phylogeny, homology is tested by Patterson's tests of similarity, conjunction, and congruence. In Hylocomiaceae erect leaves without plication and absent of foliose pseudoparaphyllia are found to be symplesiomorphies; at the infrafamilial level erect capsules with reduced peristomes are homologous (i.e., derived from a recent common ancestor). Homoplasies also provide useful insights into understanding the mechanisms of morphological evolution. A complementary methodology synthesizing adaptationist and structuralist perspectives is employed. Convergent evolution of paraphyllia in mosses is ascribed to environmental selection. The Bauplan of conducting tissue in mosses is attributed to functional constraints. Reversed evolution of central strands in *Loeskeobryum* is a manifestation of developmental constraints, which channel the variation of the ontogenetic pathway. Heterochrony by truncating (paedomorphosis) or extending (peramorphosis) the ontogenetic sequences is a common mode of morphological evolution in the Hylocomiaceae. The parallel evolution of axillary hairs by retention of juvenile morphology at the adult stage in *Hylocomiastrum, Hylocomiopsis*, and *Actinothuidium* or extending the terminal stage of ancestral state in *Hylocomium, Gollania*, and *Rhytidium* is ascribed to morphological constraints.

KEY WORDS: Hylocomiaceae, Character concept, Cladistics, Monophyly, Ontogenetic transformations, Phylogeny.

INTRODUCTION

The development of cladistics (Hennig, 1966) has offered a powerful tool not only for reconstruction of phylogeny, but also for studies of morphological evolution (cf. Wake, M., 1992), adaptation (Baum and Larson, 1991), and ecological genetics (Real, 1994). Morphology provides useful information for developmental biology, genetics, behavior, and systematics. Morphological data may contain many homoplasies, especially when large numbers of taxa are considered (Sanderson and Donoghue, 1989), thus making phylogenetic inferences ambiguous. However, two recent advances have changed current evolutionists' viewpoints on the utility of morphology for phylogenetic inference. First, homoplasies have been found not only in morphological characters, but also in gene sequences, such as *rbcL*

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(*cf.* Avise, 1994). In some instances no significant differences in the frequency of homoplasies between morphological and molecular data appear (Sanderson and Donoghue, 1989). Second, homoplasies are not as uninformative as previously believed, but provide useful insights into understanding the mechanisms of morphological evolution (Wake, 1991). Wake (1992) terms the recent developments of morphological analysis a 'renaissance', which incorporates theory and new techniques of morphology, ontogeny, and systematics for studies of comparative evolution. Cladistic techniques have played an important role for testing and falsifying hypotheses, which are critical for scientific inferences (the hypothetico-deductive method of Mayr, 1982).

In studies of systematics and morphology, homology has been one of the most important and controversial issues, ever since the term was first defined (Owen, 1843). Darwin's concept of common ancestry (Darwin, 1859) is the basis for homology theory. Consideration of homology has been shifted from merely comparing similarity of ontogeny to the development of an understanding of the patterns and processes of the continuity of information (van Valen, 1982; cf. Hall, 1992). Homology has become a phylogeny-based concept especially in the cladistic school (Stevens, 1984). Patterson (1982) synonymizes (taxic) homology with synapomorphy, which diagnoses monophyletic groups, and he proposed three tests for homology: similarity, conjunction, and congruence (de Pinna, 1991).

Although similarity of development is not the only criterion in assessing homology, ontogeny is still a sufficient factor for understanding the biology of homology (Wagner, 1989a; Wagner and Misof, 1993) and systematics (de Queiroz, 1985). Morphology of the adult stage is only the last stage of a developmental sequence (Mason, 1957). Using adult morphology will lead to the loss of information on the overall life cycle (de Queiroz, 1985). The incorporation of ontogenetic information in a phylogenetic context has been appreciated and emphasized by current systematists (Humphries, 1988; Fink, 1988; Kluge and Strauss, 1985). Although most empirical studies have been conducted on animals (e.g., Minelli and Peruffo, 1991), botanists have started paying attention to the synthesis of ontogeny and systematics (Diggle, 1992). Several pioneering studies have been carried out on fungi (Hibbett *et al.*, 1993) and plants, including *Poa* (Kellogg, 1990), *Abies* (Robson *et al.*, 1993), the order Piperales (Tucker *et al.*, 1993), cucurbits (Jones, 1992).

Combining ontogeny and traditional morphological data will be an exceptionally useful approach for phylogeny reconstruction and the study of morphological evolution (Chiang, 1994, 1995). The patterns of changing ontogenetic transformations and developmental timing (heterochrony) (Gould, 1977) have provided evolutionists with insights into how morphology evolved in different organisms. The process causing heterochrony (repatterning) of ontogeny has been an important means by which evolutionary novelties are introduced (Gould, 1988; Wake and Roth, 1989). For better understanding the evolution of morphological features, a complementary methodology, based on the distribution of heterochrony on cladograms (i.e., homology or homoplasy), synthesizing the internalist (developmental constraints) and externalist (natural selection) perspectives is recommended.

Mosses are ideal subjects for studying development and evolution. Not only are they small and easy to culture in the laboratory (Sargent, 1988; Nehira, 1988), but they also have relatively simple morphological structures (Mishler and Luna, 1991). Bryologists have already noted that developmental information is instructive for the systematics of mosses (Chiang, 1995). For example, Koponen (1968) catalogs two types of rhizoids, micronemata and macronemata, in the Mniaceae, based on their origin, topology, and branching pattern (Crundwell, 1979). *Tortula* is another moss genus that has had its systematics reconstructed

based on ontogeny of leaves and leaf-cells as well as other morphological characters (Mishler, 1986). Several morphological structures of mosses remain enigmatic, and the ontogenetic approach could be highly informative. Paraphyllia, appendages on stems, are one of the most distinctive characters in the pleurocarpous mosses. Most classifications, in effect, assume that paraphyllia evolved several times, since the paraphyllia-bearing taxa have never been grouped together, but rather are scattered in different families. Ireland (1971) hypothesized that filamentous and foliose paraphyllia were evolved from foliose pseudoparaphyllia, structures around branch primordia. In contrast, Buck (1984) argued that there is no support for the ancestor-descendant relationship between paraphyllia and pseudoparaphyllia. Regardless, the hypotheses have never been tested in any evolutionary or systematic context.

Homology of paraphyllia in the Hylocomiaceae, an ancient (Miller, 1984: Delcourt and Delcourt, 1991) and widespread family with dioecious sexuality, is also controversial. The uncertainty of the homology of paraphyllia has made bryologists propose different circumscriptions of this family. Andrews (1954) and Noguchi (1972) define Hylocomiaceae as a family bearing "horn-like" paraphyllia. Nishimura et al. (1984) added *Orontobryum,* a genus having foliose paraphyllia, to this family, based on the "present-absent" criterion. Buck (1980) argues that merely using paraphyllia to define a family is not valid, therefore, he redefines Hylocomiaceae as having a combination of characters, such as peristome ornamentation, costa number, and leaf margins. Rohrer (1985) uses growth-forms to differentiate Hylocomiaceae from its relatives. Nevertheless, growth-form seems to be an artificial and subjective category. For example, the growth-form of *Rhytidiadelphus triquetrus* is described as "mats" by Crum and Anderson (1981), and as "wefts" by Rohrer (1985). Recently, Buck and Crum (1990) transferred *Actinothuidium* and *Hylocomiopsis* into the Hylocomiaceae based on the morphology of paraphyllia. There has been no consensus on the circumscription of the Hylocomiaceae since the family was created by Fleischer (1914).

This research has four goals: 1) to reconstruct the phylogeny of the Hylocomiaceae based on ontogenetic and morphological characters; 2) to reveal ontogenetic transformations and heterochronies of morphological characters in mosses; 3) to test the homology of paraphyllia within the Hylocomiaceae and between the Hylocomiaceae and related families; 4) to interpret morphological evolution in the mosses by employing complementary methodology (Wake and Larson, 1987).

MATERIALS AND METHODS

Ingroups and outgroups

Twenty-one species of the hypothetical ingroups, *Hylocomium* B. S. G., *Hylocomiastrum* Fleisch., *Loeskeobryum* Fleisch., *Rhytidiadelphus* Warnst., *Neodolichomitra* Nog., *Pleurozium* Mitt., *Rhytidiopsis* Broth., *Rhytidium* Kindb., *Leptocladiella* Fleisch., *Macrothamnium* Fleisch., *Leptohymenium* Schwaegr.,*Orontobryum* Fleisch., and *Miehea* Ochyra, were studied. In order to test the hypotheses on phylogenetic relationships of the Hylocomiaceae within the mosses, 22 species (Table 1) of 11 related families were sampled as outgroups: Thuidiaceae, Theliaceae, Climaceaceae, Leskeaceae, Anomodontaceae, Hypnaceae, Plagiotheciaceae, Brachytheciaceae, Leucodontaceae, Amblystegiaceae and Entodontaceae (cf. Buck and Vitt, 1986).

Species found in North America, including *Rhytidium rugosum* (Hedw.) Kindb., *Rhytidiadelphus squarrosa* (Hedw.) Warnst., *R. loreus* (Hedw.) Warnst., *R. triquetrus*

(Hedw.) Warnst., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B. S. G., *Hylocomiastrum pyrenaicum* (Spruce) Fleisch., *H. umbratum* (Hedw.) B. S. G., *Loeskeobryum brevirostre* (Brid.) Fleisch., and *Rhytidiopsis robusta* (Hook.) Broth., were collected in the Smoky Mountains and in the Northwest Pacific region of the United States. Specimens of these taxa deposited at the Missouri Botanical Garden were also examined. Specimens of Asiatic species, including *Hylocomiastrum himalayanum* (Mitt.) Broth., *Loeskeobryum cavifolim* (Lac.) Fleisch., *Macrothamnium macrocarpum* (Reinw. and Hornsch.) Fleisch., *M. javense* Fleisch., *Leptohymenium tenue* (Hook.) Schwaegr., *Leptocladiella psilura* (Mitt.) Fleisch., *Neodolichomitra yunnanensis* (Besch.) Kop. and *Orontobryum hookeri* (Mitt.) Fleisch. were borrowed from the Natural History Museum, London; the Farlow Herbarium, Harvard University; the Rijksherbarium, Leiden; Hattori Botanical Laboratory; Hiroshima University; and Herbarium, Institute of Botany, Academia Sinica, Beijing (Appendix 1).

Ontogenetic analyses

The ontogenetic transformations of three features - paraphyllia, axillary hairs, and central strands - were examined and interpreted. Most observations were from herbarium specimens. Eight to ten specimens were sampled for each species. Central strands were determined from cross sections of branches and stems. The earliest stage of each character was determined from juvenile buds or near the meristems of stem or branch tips. In most cases ontogeny began with a single cell or uniseriate row of cells. Later stages were observed along the branches and stems. The criterion used to arrange the developmental stages from juvenile to maturity was that features had to develop from simple to complex structures in terms of size and branching number. Ontogenetic data were incorporated into the phylogenetic analysis. The whole ontogenetic transformation was recognized as a single character. Variations on transformations were placed into different character states. Different states of each character were coded and polarized by outgroup comparisons (Watrous and Wheeler, 1981). The multistate characters were treated as unordered.

Characters

Thirty-two morphological characters, six sporophytic and 26 gametophytic, were scored under a stereo light microscope.

1. *Paraphyllia*: Nine types of paraphyllia were classified based on their ontogenetic transformations (Fig. 1). Ten states were coded: **0**, absent; **1**, deer-horn; **2**, reindeer-horn; **3**, ox-horn; **4**, triangular; **5**, linear; **6**, foliose; **7**, lanceolate; **8**, lacinate; **9**, filiform.

2. *Papillosity on paraphyllia*: The cell-surface of some paraphyllia is papillose. Only two outgroup genera have this character. Being papillose was interpreted as the primitive state and coded as **0.**

3. *Pseudoparaphyllia*: Pseudoparaphyllia are one of the most ill-defined characters in pleurocarpous mosses. Here, pseudoparaphyllia are considered in a strict sense, which defines pseudoparaphyllia as appendages around branch primordia differing in shape from the latter. Three types of pseudoparaphyllia are described: foliose type, which exists in some outgroups (*e.g., Gollania*); "curious leaf" type which is larger in size compared to the former (*cf.* Noguchi, 1972) and exists both in some ingroups (such as *Hylocomiastrum*) and outgroups (e.g., *Actinothuidium*); lanceolate type, only in two outgroup genera (*Antitrichia, Hygrohypnum*). Four states were coded: **0**, foliose; **1**, curious-leaf; **2,** lanceolate; **3**, absent.

4. *Growth form*: Most ingroups, except *Pleurozium*, *Rhytidiadelphus*, and *0rontobryum*, have sympodial growth form; plants grow by lateral innovations instead of terminal meristems on stem-tips. All the outgroups have monopodial growth-form. Two states were coded: **0**, monopodial; **1**, sympodial.

5 *Central strands*: The examination of ontogeny reveals three types of central strands (discussed in detail in the results). Central strands are absent (state **2**) in *Hylocomium splendens*, *Leptocladiella psilura* (ingroups), *Actinothuidium*, *Hylocomiopsis* (the Thuidiaceae), *Anomodon*, *Haplohymenium* (the Leskeaceae), and *Antitrichia* (the Leucodontaceae). Two types of transformations were interpreted as early (state **0**) and late (state **1**) central strand.

6. *Branching patterns*: Three types of branching patterns were described: primarily pinnately branching (**0**), secondary pinnately branching (**1**), and tree-like branching (**2**). The first two types were found both in ingroups and outgroups. The tree-like branching was only found in *Climacium* (Climaciaceae).

7. *Differentiation of branch and stem leaves*: Stem and branch leaves are differentiated in most ingroups except five genera (*Rhytidiopsis*, *Rhytidium*, *Rhytidiadelphus*, *Orontobryum*, and *Leptohymenium*). In contrast, differentiated leaves are absent in most outgroups, except the Brachytheciaceae, Hypnaceae, and Thuidiaceae. Two states were coded: **0**, absent; **1**, present.

8. *Costa number of stem-leaves*: In most taxa leaves have either single or double costa. However, in *Neodolichomitra yunnanensis* and *Antitrichia curtipendula* the development of stem leaf costa is not canalized; single, double, or forked costa can be observed in single individuals. In addition, no costae were differentiated in *Myurella*. Four states were coded: **0**, single; **1**, double; **2**, forked; **3**, absent.

9. *Costa number of branch-leaves*: *Antitrichia,* and *Leptocladiella psilura* have uncanalized leaf-costa. Three states were coded: **0**, single; **1**, double; **2**, forked; **3**, absent.

10. *Costal spine*: Three ingroup genera (i.e., *Rhytidium*, *Hylocomiastrum*, and *Leptocladiella*) and *Eurhynchium* (outgroup) bear spines at the ends of costa. Two states were coded: **0**, absent; **1**, present.

11. *Stem leaf apex:* Most outgroups have acuminate stem-leaf apices. *Pleurozium*, *Neodolichomitra* (ingroup), and *Anomodon* have a round apex; *Macrothamnium* and related genera have an apiculate apex from a round leaf body. A caudate apex was observed in *Hylocomium splendens*. Four states were coded: **0**, acuminate; **1**, apiculate; **2**, caudate; **3**, round.

12. *Leaf-base:* Three states were coded: **0**, decurrent; **1**, not decurrent; **2**, auriculate. The auriculate bases were observed from species of *Loeskeobryum*, *Rhytidiadelphus*, and *Anomodon*.

13. *Leaf-apex margins:* Two states were coded: **0**, plane (most taxa); **1**, recurred (*Pleurozium*, *Hygrohypnum*).

14. *Leaf plication:* The surface of leaves of most taxa is without wrinkles (**0**). Two types of plication were described: longitudinal (**1**) (e.g., *Rhytidium*, *Ptilium*) and transverse (**2**) (*Gollania ruginosa*).

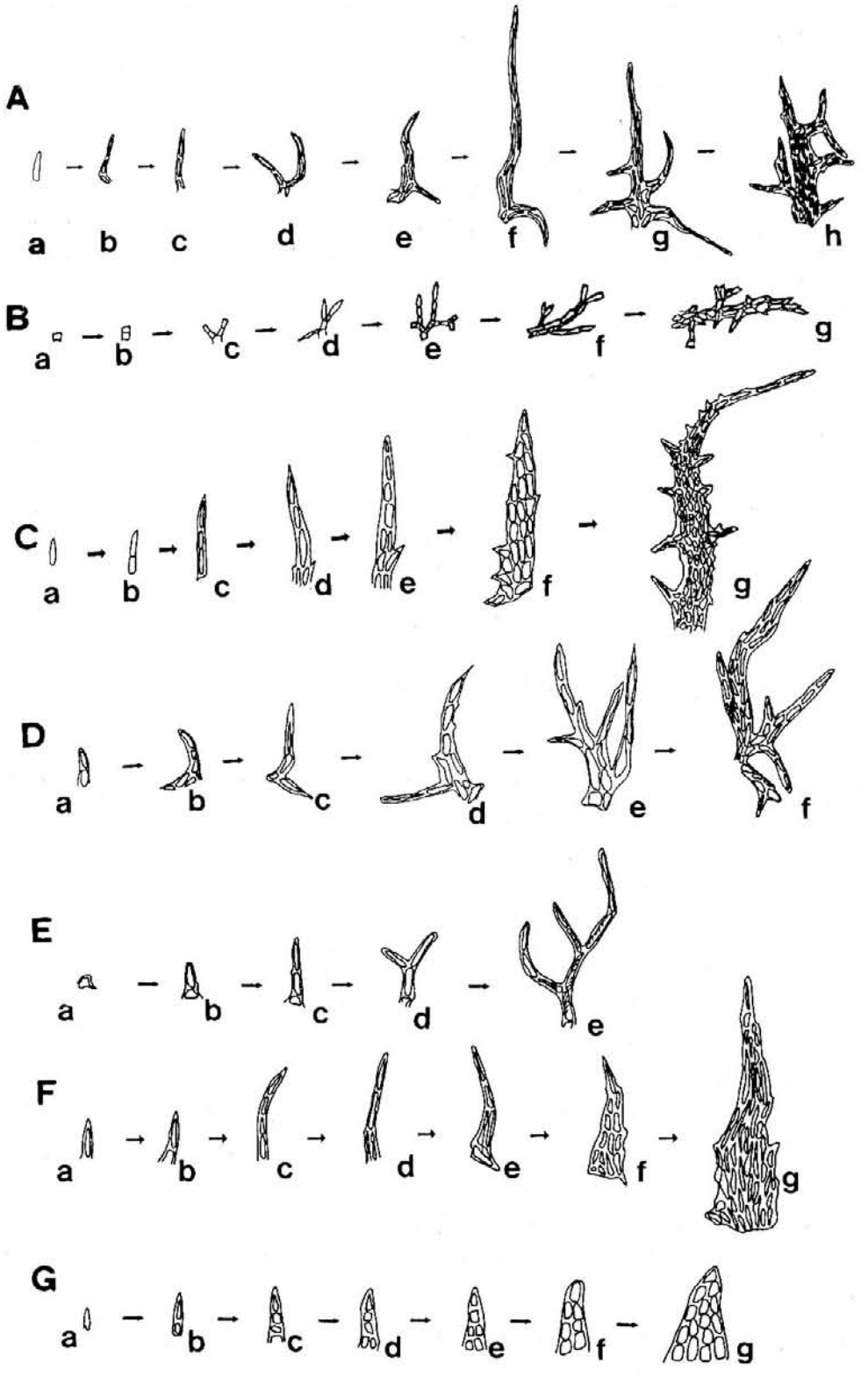


Fig. 1. Ontogenetic transformations of paraphyllia in mosses. A. horn-like paraphyllia; B. linear paraphyllia; C. lacinate paraphyllia; D. foliose paraphyllia; E. filiform paraphyllia; F. triangular paraphyllia; and G. lanceolate paraphyllia.

15. *Leaf orientation*: All ingroups, except for *Leptocladiella flagellaris* (**0**), and most outgroups have erect leaves (**1**). Secund leaves (**0**) were described from three taxa of the Hypnaceae.

16. *Spread of leaves*: There are two different ways that leaves spread from the branches or stems. Most taxa have leaves with tips pointing to the stem-apex (state **0**). Leaves of *Rhytidium*, *Rhytidiopsis*, and *Rhytidiadelphus loreus* and *R. squarrosa* are reflexed (state **1**).

17. *Neck of leaves*: *Loeskeobryum*, *Haplohymenium*, and *Anomodon* (except for *A. minor*) have leaf necks. Two states were coded: **0**, absent; **1**, present.

18. *Leaf-cells*: All ingroups and some outgroups (e.g., *Ptilium*, *Miehea*) have lanceolate leaf-cells. Rhomboidal cells were found in *Antitrichia.* Rectangular leaf cells were observed from the rest of the outgroups. Three states were coded: **0**, rectangular; **1**, lanceolate; **2**, rhomboidal.

19. *Alar cells*: Three states of cells at the corners of the leaf base were coded: **0**, alar cells not different from basal cells; **1**, alar cells differentiated and different from basal cells; **2**, alar cells not differentiated

20. *Cell papillosity*: The surface of the cell wall may be smooth (**3**) or papillose. Five types of papillae were observed: regular-sized papilla at the front corner of cells (**0**); regular-sized mixed with some enlarged papilla at the front corner of cells (**1**); enlarged papilla at the corner of cells (**2**); single papilla on the cell-wall (**4**); multiple papilla on the cell wall (**5**); single papilla with branched tips on the cell-wall (**6**).

21. *Leaf-margins*: Five states were coded: **0**, entire; **1**, crenulate; **2**, crenate, tooth with one cell; **3**, dentate, tooth with two to three cells; **4**, ciliate.

22. *Annual buds*: Annual buds occur in *Hylocomium* and *Neodolichomitra*. Two states were coded: **0**, absent; **1**, present.

23. *Sexuality*: *Entodon* (Entodontaceae) and *Helodium* (Thuidiaceae) are monoecious (**0**). Phyllodiecious sexuality with epiphytic, dwarf males (**2**) (Wyatt, 1985) was reported from *Thelia* and *Macrothamnium javense*. Most taxa are dioicous (**1**).

24. *Capsule inclination*: Mature capsules may be inclined (**0**) or erect (**1**) in both ingroups and outgroups.

25. *Annulus*: Two states were coded: **0**, absent; **1**, present.

26. *Operculum*: The operculum may be conic (**0**) or rostrate (**1**) in both ingroups and outgroups.

27. *Exostome ornamentation*: Four types of ornamentation on exostomes were described: papillose (**0**), striate (**1**), reticulate (**2**), smooth (**3**).

28. *Endostome*: Most taxa have well-differentiated endostomes (**0**). Incomplete endostomes (**1**) were found in *Macrothamnium leptohymenioides*. Residual endostomes (**2**) were observed in *Orontobryum*, *Leptohymenium*, and some outgroups.

29. *Cilia*: Two states were coded: **0**, absent; **1**, differentiated.

30. *Stoloniform stem*: Creeping, stoloniform primary stems were only found in *Anomodon* and *Haplohymenium*. Two coded states: absent (**0**), present (**1**).

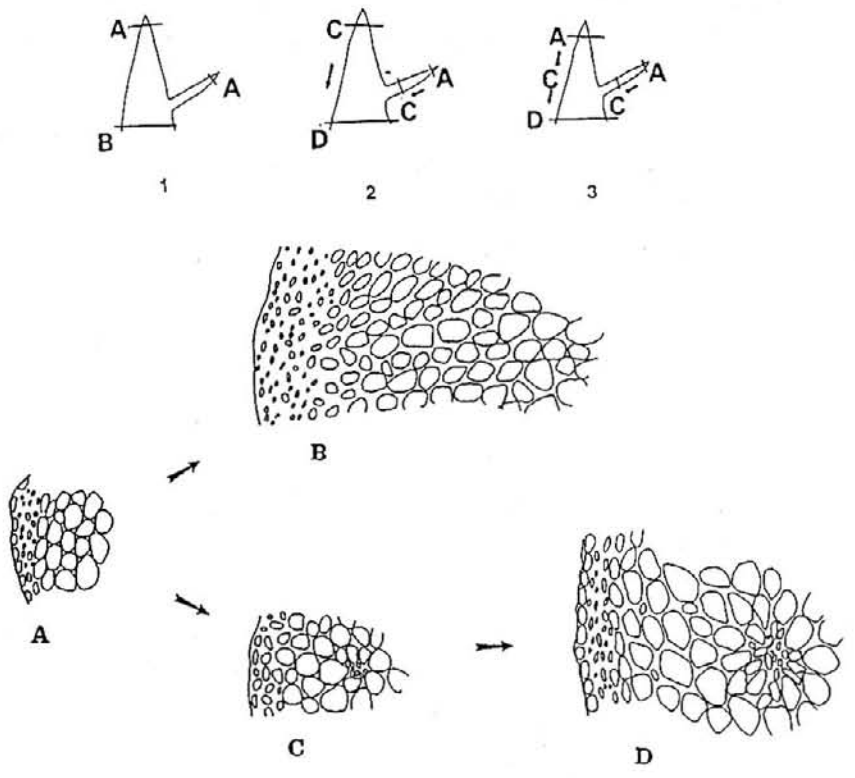
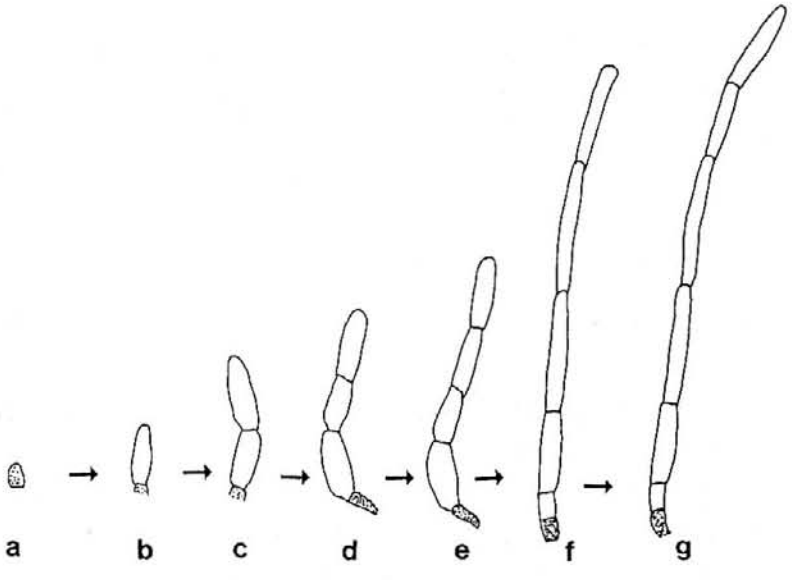


Fig. 2. Ontogenetic transformations of central strands: A → B, central strands absent; A → C → D, differentiation of central strands. 1-3 (above the ontogenetic sequences): states of ontogeny of central strands: 1, absent; 2, early central strand; and 3, late central strands.



31. *Rhizoids*: Two states were coded: **0**, not frequent; **1**, abundant.

32. *Axillary hairs* (Fig. 3): Five states were coded based on the number of apical cells: **0**, three; **1**, two; **2**, four; **3**, five; **4**, six. The ontogenies of the axillary hairs are discussed in detail below.

Phylogenetic analyses

In order to reconstruct the phylogeneny of the Hylocomiaceae and related families, cladistic analyses based on parsimony were performed. Heuristic searches on a data matrix (Table 1) of morphological and ontogenetic data with TBR branch swapping, with stepwise addition of 10 random replicates, were undertaken using the PAUP computer program (Version 3.1.1, Swofford, 1993). All characters were unweighted. Trees were rooted in all

Table 1. Morphological and ontogenetic characters of hypothetical ingroups of Hylocomiaceae and outgroups. Characters and character states see contexts.

Taxa \ Characters	0 5	1 0	1 5	2 0	2 5	3 0	3 2
Hypothetical ingroups:							
Hylocomium splendens	10212	11110	21001	00102	21101	12010	04
Hylocomiastrum umbratum	20111	11111	00001	00103	30100	01010	01
Hylocomiastrum himalayanum	20111	11001	01001	00103	30100	01010	01
Hylocomiastrum pyrenaicum	20111	01001	01001	00103	30100	01010	01
Loeskeobryum brevirostre	30211	01110	02001	01103	20101	11010	00
Loeskeobryum cavifolium	30211	01110	01001	01103	20101	11010	00
Rhytidiopsis robusta	30100	00110	01011	10103	20101	01010	00
Rhytidium ruginosa	00100	00001	01011	10112	20101	01010	03
Pleurozium schreberi	00200	01110	31101	00113	00100	02010	04
Neodolichomitra yunnanensis	00210	11210	30001	00103	01101	01010	01
Rhytidiadelphus triquetrus	00200	00110	02011	00102	20101	02010	00
Rhytidiadelphus loreus	00200	00110	01011	10103	20101	01010	00
Rhytidiadelphus squarrosa	00200	00110	01001	10103	20101	01010	00
Macrothamnium macrocarpum	00210	11110	10001	00100	30101	01010	00
Macrothamnium javense	00210	11110	10001	00100	30201	01010	00
Macrothamnium leptohymenioides	00210	11110	10001	00100	30110	01100	00
Leptohymenium tenue	00210	10110	10001	00100	20110	13200	00
Orontobryum hookeri	40100	00110	10001	00103	30110	01200	00
Leptocladiella psilura	00212	01121	00001	00103	10101	11010	00
Leptocladiella flagellaris	00000	01110	01000	00103	10101	01010	00
Miehea himalayanum	40200	00000	01001	00103	101??	????0	10
Outgroups:							
Gollania ruginosa	00000	01110	00020	00100	20101	01010	03
Ptilium crista-castrensis	00000	01110	01010	00103	20101	01010	00
Thuidium cymbifolium	51200	11000	01001	00004	10101	01010	01
Actinothuidium hookeri	60102	01000	01011	00105	201??	????0	01
Hylocomiopsis ovacarpa	60102	01000	01011	00101	20110	11000	01
Leskea gracilescens	70200	00000	01001	00004	10111	00000	01
Anomodon minor	00202	00000	31001	00005	10111	11001	10
Anomodon viticulosus	00202	00000	31001	01005	10111	11001	10
Anomodon rugelii	00202	00000	32001	01005	10111	11001	10
Anomodon attenuatus	00202	00000	31001	01005	10110	11001	10
Thelia hirtella	80200	00000	01001	00004	30210	00100	10
Thelia asprella	81200	00110	00001	00006	40210	00100	10
Thelia lescurii	80200	00000	01001	00006	40210	00100	10
Haplohymenium triste	00202	00000	01001	01005	10110	11001	10
Myurella sibrica	00200	00330	31001	00003	00111	01010	12
Entodon seductrix	00200	00110	01001	00113	10011	11000	02
Eurhynchium pulchellum	00200	01001	00001	00103	10101	01010	00
Climacium dendroides	90210	20000	01011	00103	30110	10000	10
Hygrohypnum sp.	00301	00110	00101	00103	10101	01010	03

analyses using outgroups from eleven families. Strict (Sokal and Rohlf, 1981) and 50% majority-rule (Margush and McMorris, 1981) consensus trees were determined and used to assess both the monophyly of the Hylocomiaceae and morphological evolution.

A g*1* test (Huelsenbeck, 1991) of skewed tree-length distributions was calculated from 10,000 random trees generated by PAUP in order to measure the information content of the data. Critical values of the g*1* test are given in Hillis and Huelsenbeck (1992). The fit of character data on phylogenetic hypotheses (Swofford, 1991) was evaluated and calculated by the consistency index (CI) (Kluge and Farris, 1969) and retention index (RI) (Archie, 1989; Farris, 1989). The statistical significance of CI was determined according to Klassen *et al.* (1991). The confidence of the clades were tested by bootstrapping (Felsenstein, 1985) with 400 replicates (Hedges, 1992) of heuristic searches on the 50% majority rule trees. The nodes with bootstrap values greater than 0.70 are significantly supported with ≥ 95% probability (Hillis and Bull, 1993).

Tests of taxonomic hypotheses

Statistically the inferred phylogeny based on parsimony does not necessarily reject other taxonomic hypotheses with additional steps on cladograms. The significance of the differences between the shortest trees and the alternative trees based on other specific hypotheses, such as homology of paraphyllia, can be tested by a nonparametric Wilcoxon signed-rank test (Templeton, 1983). Alternative trees are constructed by using the TOOLS option of the MacClade program (Maddison and Maddison, 1992). The COMPARE 2 TREES option of the MacClade program was used to provide information of the number of characters favoring each tree of a pair (O'Kane, 1993). The statistical significance of the tests was determined by Table A1 and Table A2 of Hollander and Wolfe (1973).

Tests of homology

Homology is synonymous with synapomorphy (Patterson, 1982). Three tests were conducted to test the hypotheses of homology: similarity, conjunction, and congruence tests (Patterson, 1982; de Pinna, 1991). "Similarity" basically follows Geoffroy's compositional and typographical similarity (cf. Panchen, 1992) as well as ontogenetic similarity. "Conjunction" is failed if two proposed homologues occur together in a single organism. "Congruence" is the most powerful test (Patterson, 1982), in which two characters support a nested hierarchical relationship of subclades within a clade.

RESULTS AND DISCUSSION

Phylogenetic inference

Two equally most parsimonious trees of 167 steps, with CI of 0.41 ($p < 0.05$) , RI of 0.691, and g1 of -0.37 ($p < 0.05$), were identified by cladistic analyses on ontogenetic and morphological data. The clade of Hylocomiaceae contains three subclades (Fig. 4): subclade *Hylocomium* (*Hylocomium, Loeskeobryum, Leptocladiella*); subclade *Hylocomiastrum* (*Hylocomiastrum, Neodolichomitra*); and subclade *Macrothamnium* (*Macrothamnium, Leptohymenium, Orontobryum*). Hypnaceae (*Gollania* and *Ptilium*) is the family most closely related to Hylocomiaceae. A single most parsimonious tree of the Hylocomiaceae rooted at the Hypnaceae (Fig. 5) was identified with 59 steps, CI of 0.73 ($p < 0.05$), RI of 0.754, and g1 of -0.72 ($p < 0.05$). The monophyly of the family was statistically supported

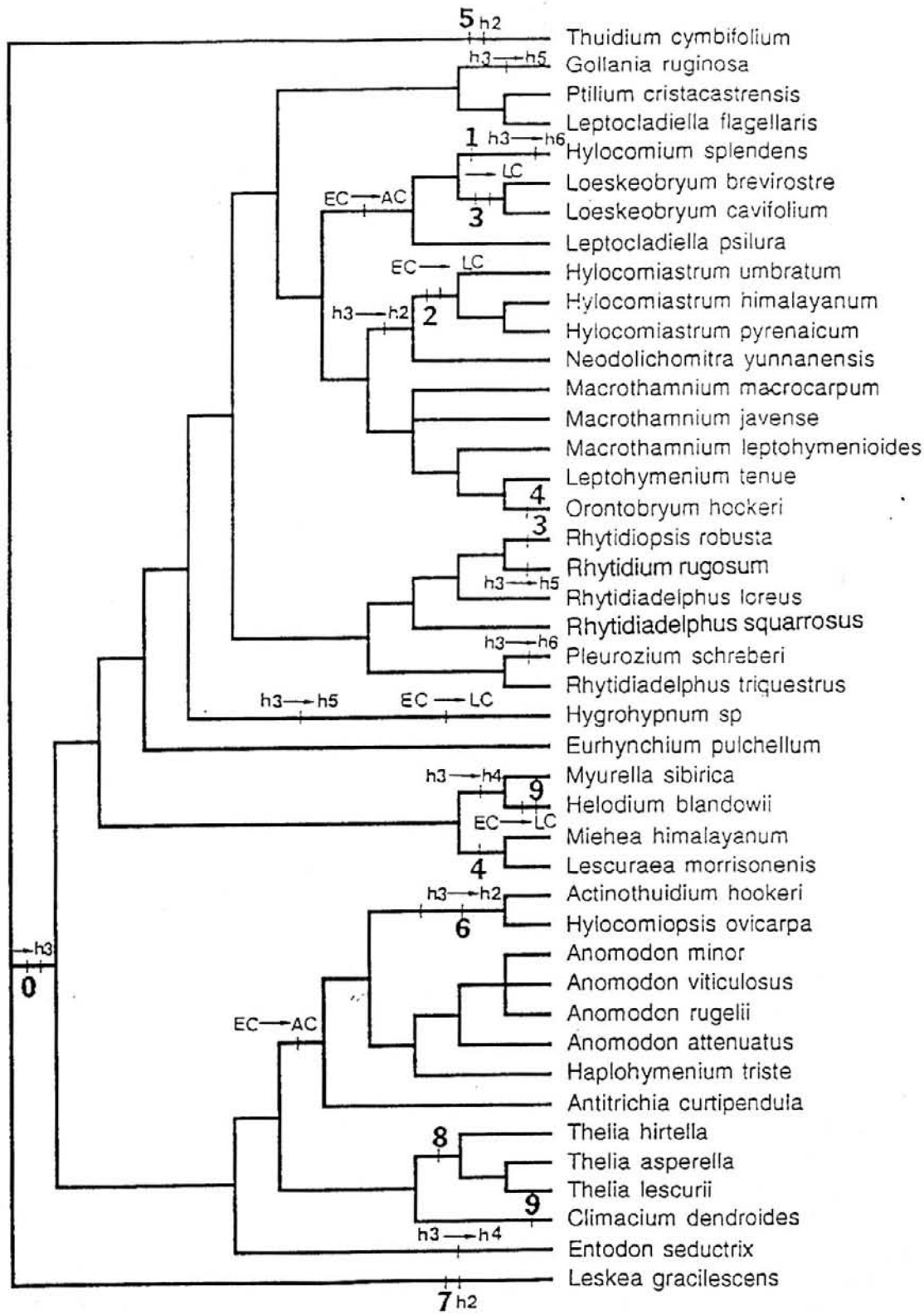


Fig. 4. Strict consensus tree identified by PAUP. 0-9, types of paraphyllia. Evolution of characters, including different number of apical cells of the axillary hairs (i.e., h2 to h6), and types of central strands (AC, central strands absent; EC, early central strands; and LC, late central strands), are indicated at nodes.

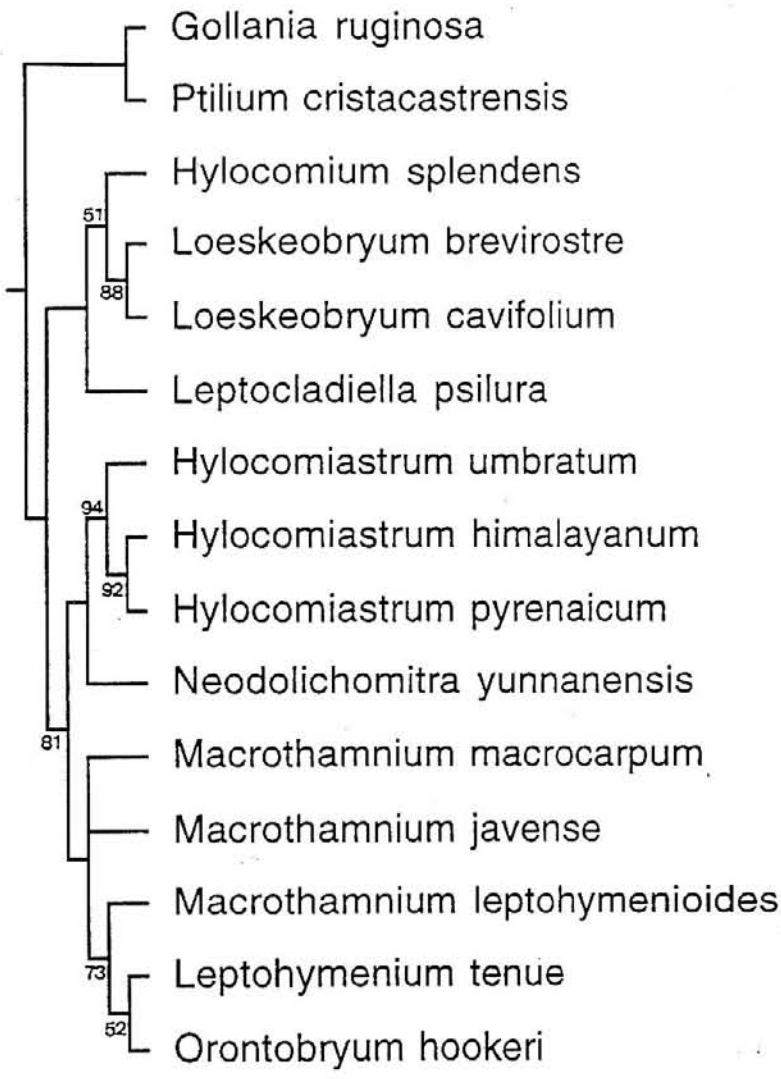


Fig. 5. Consensus tree of Hylocomiaceae rooted at *Gollania* and *Ptilium* with bootstrap values at nodes.

with bootstrap value of 0.81. The node of *Macrothamnium leptohymenioides*, *Leptohymenium*, and *Orontobryum* was significantly supported with bootstrap value of 0.73; two genera, *Loeskeobryum* (bootstrap value = 0.88) and *Hylocomiastrum* (bootstrap value = 0.94), were highly supported. The node of *Leptohymenium* and *Orontobryum* with a bootstrap value of 0.52 was not significantly supported.

Like many other moss families (Chiang, 1994), the Hylocomiaceae is not convincingly diagnosed by any synapomorphy due to the high frequency of homoplasy. Erect leaves without plication and the lack of foliose pseudoparaphyllia are shared by ingroup taxa as well as most outgroups, except for Hypnaceae, and appear to be plesiomorphies. One peculiar character in the family is the sympodial growth-form. However, a reversal of monopodial growth type occurred in *Orontobryum*. At the intrafamilial level, the subclade *Hylocomiastrum* is characterized by axillary hairs with two apical cells; the subclade *Macrothamnium* is characterized by broad leaves with apiculate apices; and the subclade *Hylocomium* is characterized by a rostrate operculum. Within the subclades *Hylocomiastrum*, the genus *Hylocomiastrum* is recognizable by having reindeer-horn paraphyllia and costa

spines; *Loeskeobryum* has leaves with necks and ox-horn paraphyllia; *Leptocladiella* has branch-leaves with forked costa; *Hylocomium* has reticulate exostome ornamentation and stem-leaves with caudate apices; *Neodolichomitra* has leaves with round apices and entire margins. The clade of *Macrothamnium leptohymenioides*, *Leptohymenium*, and *Orontobryum* is well-diagnosed by erect capsules with reductive sporophytic characters; the clade of *Leptohymenium* and *Orontobryum* is characterized by undifferentiated leaves (cf. Chiang, 1995). In addition, *Orontobryum* is recognized by having triangular paraphyllia, and monopodial growth-form; *Leptohymenium* is recognized by having smooth exostome ornamentation.

Based on the consensus tree, *Rhytidium*, *Rhytidiopsis*, *Rhytidiadelphus*, and *Pleurozium* were excluded from Hylocomiaceae. Two equally parsimonious trees (29 steps; Fig. 6) of the Rhytidiaceae, comprising the above four genera, were identified rooted at Hypnaceae, with a CI of 0.82 ($p < 0.05$), RI of 0.62, and $g1$ of -0.79 ($p < 0.05$). The family was significantly supported with a bootstrap value of 82%. The clade of *Rhytidiopsis* and *Rhytidium* was also highly supported with a bootstrap value of 72%. In contrast, the monophyly of *Rhytidiadelphus* was rejected because no shared derived characters were found. That is, *Rhytidiadelphus* appears to be a paraphyletic group.

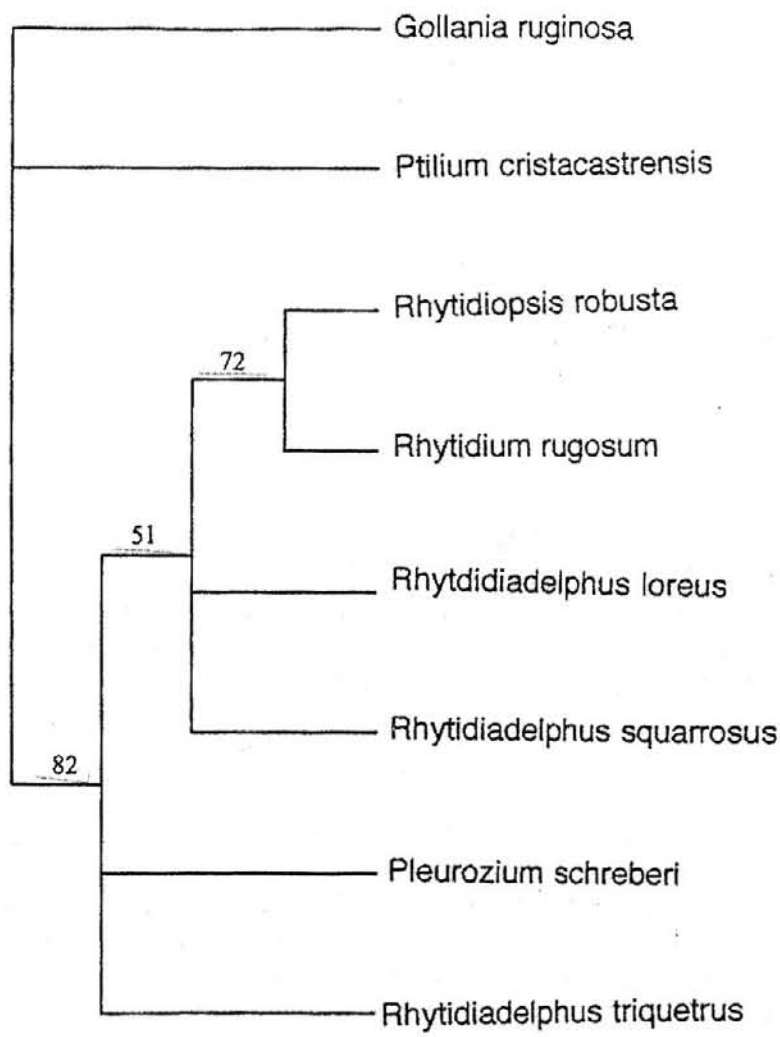


Fig. 6. Consensus tree of Rhytidiaceae rooted at *Gollania* and *Ptilium* with bootstrap values at nodes.

Tests of taxonomic hypotheses

Rohrer (1985) suggests a classification of the Hylocomiaceae consisting of twelve genera, i.e., the above Hylocomiaceae plus the Rhytidiaceae. An alternative tree with one more step (Fig. 7), in which the clade of four genera of Rhytidiaceae is a sister group toe Hylocomiaceae, is not significantly different from the parsimonious tree ($p< 0.25$, Table 2). Thus, the phylogenetic hypothesis of Rohrer (1985) is not rejected. Another alternative hypothesis, which suggests a monotypic family Rhytidiaceae with the most closely related family being Brachytheciaceae (cf. Buck and Vitt, 1986), is also not rejected by a signed-rank test (Table 2).

Table 2. Wilcoxon ranked-sign test for alternative taxonomic hypotheses.

Alternative hypothesis	Further steps	Number of characters favoring shortest tree	Number of characters favoring alternative tree	Statistics
1. Rohrer (1985)	1	2	0	n.s.
2. Noguchi (1972)	7	7	1	*
3. Nishimura *et al.* (1984)	13	12	2	**
4. Buck and Vitt (1986)	3	6	3	n.s.
5. Buck and Crum (1990)	5	7	2	n.s.
6. Ochyra (1989)	8	8	0	**
7. Koponen & Norris (1985)	6	6	0	*
8. Watanabe (1972)	3	5	2	n.s.

*: *P< 0.05*; **: *P< 0.01*; *n.s.*: *non-significant.*

A close relationship between *Miehea*, a genus designated and placed in Hylocomiaceae based on presence of paraphyllia (Ochyra, 1989), and *Hylocomium* is not supported by the cladistic analysis and signed-rank test (Table 2). *Miehea* is related to *Lescuraea* by shared triangular paraphyllia (cf. Chiang, 1998). The taxonomic position of *Leptocladiella flagellaris* Koponen and Norris (1985) in the Hylocomiaceae is rejected (Table 2). By sharing secund leaves, foliose pseudoparaphyllia, and monopodial growth-form, *Leptocladiella flagellaris* is more related to *Ptilium* (family Hypnaceae) (cf. Chiang, 1995). Therefore, *Miehea* and *Leptocladiella flagellaris* should be excluded from the Hylocomiaceae.

The taxonomic hypotheses of Noguchi (1972) and Nishimura *et al.* (1984), which suggest paraphyllia to be the defining character for Hylocomiaceae, are rejected by the signed-rank test (Table 2). Another alternative classification, which transfers *Actinothuidium* and *Hylocomiopsis* into the Hylocomiaceae (Buck and Crum, 1990), is not rejected. The earlier classification (Watanabe, 1972), which placed two genera above in the Thuidiaceae, is also not rejected.

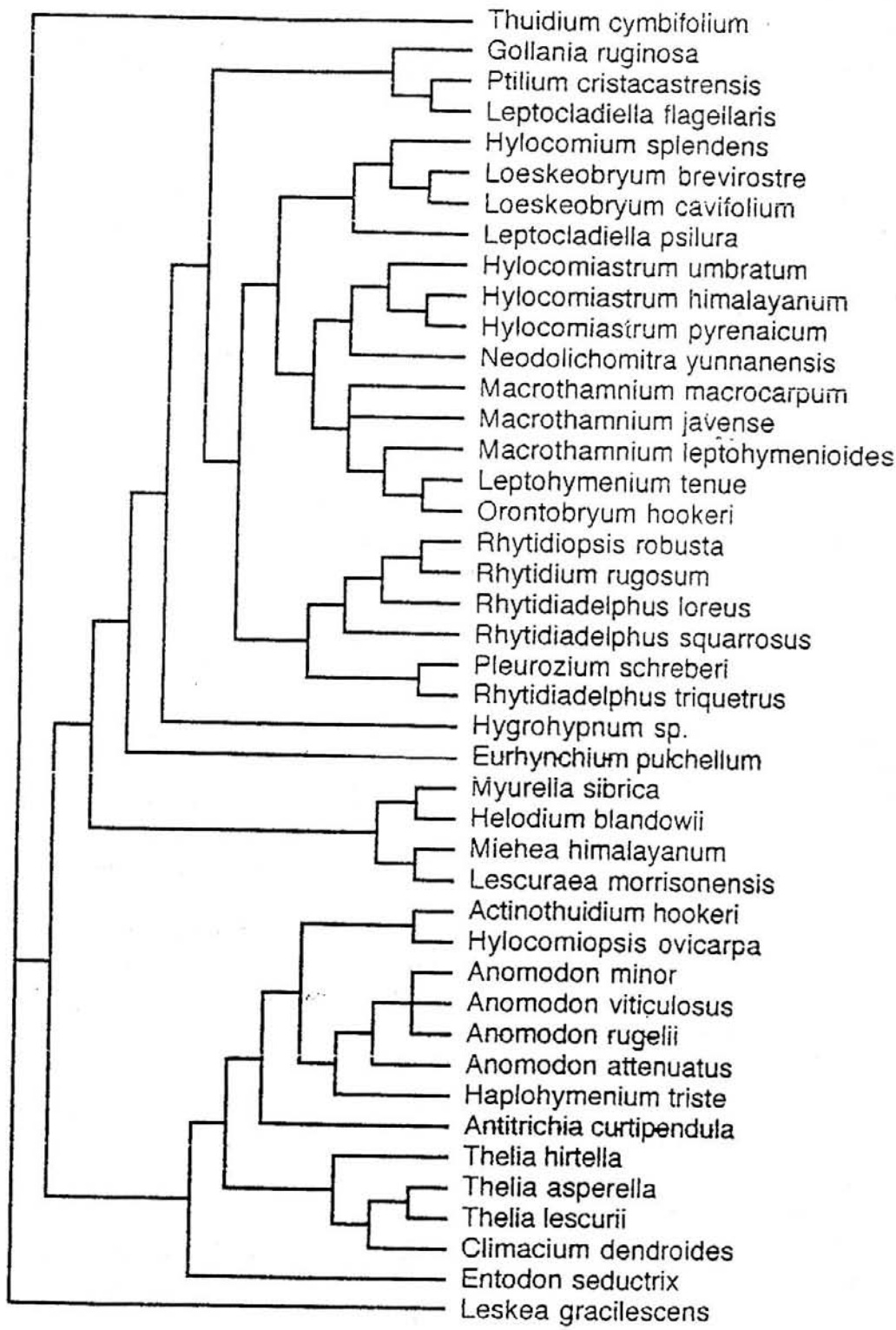


Fig. 7. An alternative phylogenetic hypothesis suggesting a monophyletic group composed by Hylocomiaceae and Rhytidiaceae.

Ontogenetic transformations and Morphological Evolution

1. Ontogenetic transformations

The ontogeny of three characters - paraphyllia, central strands, and axillary hairs – was interpreted according to the developmental sequences and the processes involved in different developmental stages.

1). Paraphyllia

All paraphyllia initiate from a single, lanceolate or rectangular cell arising from epidermal cells of stems or branches. Following the initiating stage several processes involved in the ontogenetic pathway are defined as follows: 1) elongating: cells divide transversely; 2) broadening: cells divide into two rows; 3) foliating: cells divide into three rows or more; 4) branching: small branches grow from the main body; 5) bifurcating: tips of main body separate into two branches regularly and symmetrically; 6) protruding: marginal cells project into dentate or ciliate teeth. Paraphyllia are classified into seven types according to the order and timing of developmental processes involved in the ontogenetic pathway. The names of different types are based on the shape of the terminal stage.

A. Horn-like paraphyllia (Fig. 1A): The initial cell (1A-a) elongates into a four-celled, hair-like structure (1A-c), then transforms into a fork-like stage (1A-d) by branching. The basal part broadens into double rows (ox-horn stage; 1A-f). The broadening and branching paraphyllia transform into a deer-horn stage with multi-row basal part and three to four branches (1A-g). Branches foliate into three rows or more and bear several branchlets (deer-horn stage; 1A-h). Three sub-types of horn-like paraphyllia sharing ontogenetic transformations are distinguished based on the morphology of the terminal stage.

1A. ox-horn type: Ontogeny transforms from 1A-a to 1A-f (Fig. 1). This type occurs in *Loeskeobryum* and *Rhytidiopsis*.

2A. deer-horn type: Ontogeny transforms from 1A-a to 1A-g. This type occurs in *Hylocomium*.

3A. reindeer-horn type: Ontogeny transforms from 1A-a to 1A-h. This type occurs in *Hylocomiastrum*.

B. Linear paraphyllia (Fig. 1B): Ontogeny initiates from a rectangular cell, which transforms into a single-rowed and branching structure (1B-e) by elongating and branching. Then the basal part divides into two rows. This type occurs in *Thuidium*.

C. Lacinate paraphyllia (Fig. 1C): A single, lanceolate cell (a) transforms by elongating (b, c), broadening (d), protruding (e), and foliating (f-i) into a foliose structure with lacinate margins. This type occurs in *Thelia*.

D. Foliose paraphyllia (Fig. 1D): A single, lanceolate cell (a) elongates and branches into a single-row, branching structure (b-d); and then foliates into several rows (e), and branches several times (f). This type occurs in *Actinothuidium* and *Hylocomiopsis*.

E. Filiform paraphylllia (Fig.1E): Ontogeny initiates from a colored lanceolate cell (1E-a) and transforms into 3- or 4-celled hair-like structure (1E-d). The cells of the basal part divide into two rows. The apical cell bifurcates, followed by elongation, into a clear filiform structure. This type occurs in *Helodium* and *Climacium*.

F. Triangular paraphyllia (Fig. 1F): Two processes, elongation and foliating, are involved in the ontogeny from an initial cell through a hair-like structure to a triangular terminal stage. This type occurs in *Orontobryum, Miehea,* and *Lescuraea*.

G. Lanceolate paraphyllia (Fig. 1G): This type is similar to the triangular type in shape,

but is narrower. However, the cells of lanceolate paraphyllia are rectangular instead of lanceolate. Ontogeny initiates from a rectangular cell and transforms into a lanceolate structure by broadening of the basal part. This type occurs in *Leskea*.

2). Central strands

Central strands are conducting tissue originating from the apical cells of stems or branches. In pleurocarpous mosses central strands are usually composed of homogeneous cells and are not differentiated into specific structures for water-conduction (hydroids) or food-conduction (leptoids) (Hébant, 1977). In branches the ontogeny of central strands transforms from undifferentiated tissue through earlier stage of two to three cells into a mature strand (Fig. 2). In contrast, in stems the timing of differentiation of central strands may vary. According to the developmental timing of stem central-strands, two types can be classified. In addition, in some taxa, central strands are absent.

A. "Early" type (Fig. 2A): The central strands of stems are differentiated from the tip of apex. No transformations are observed in this type. Early central strands occur in most taxa.

B. "Late" type (Fig. 2B): The pattern of differentiation of central strands in stems is similar to that in branches. Genera *Leoskeobryum, Hylocomiastrum,* and *Hygrohypnum* have late central strands (Table 1).

C. Absent: In some taxa- e.g., *Hylocomium* (Table 1)- central strands are lacking in stems and branches.

3). Axillary hairs

The ontogeny initiates from a colored, basal cell at leaf axils (Fig. 3). Clear apical cells grow on the top of basal cells by transversal division. Different numbers of apical cells at the terminal stage are found among taxa (Table 1). Most species have three apical cells. Six apical cells are observed in *Hylocomium* and *Pleurozium*; five cells are observed in *Gollania, Rhytidium*, and *Hygrohypnum*; four cells are observed in *Myurella, Helodium*, and *Entodon*; two cells are observed in *Hylocomiastrum, Actinothuidium, Hylocomiopsis, Thuidium*, and *Leskea*.

2). Morphological Evolution

Morphological characters evolve due to natural selection as well as other extrinsic forces (such as random genetic drift), internal morphological constraints, and historical phylogenetic constraints (McKitrick, 1993). In order to understand the mechanisms of morphological evolution both external (adaptation) and internal (constraints) processes need to be considered. Here a complementary methodology (Wake and Larson, 1987), which looks at the phenotypic variation from a hierarchical viewpoint, is employed.

1). Homology and evolution of paraphyllia

Based on the ontogenetic transformations (Fig. 1) paraphyllia of different types, such as horn-like paraphyllia and filiform paraphyllia, fail Patterson's similarity test by lacking a shared developmental pathway. They also fail the congruence test because no nested hierarchical relationships among paraphyllia of different types are supported by the cladistic analysis (Fig. 4). Nevertheless, they pass the conjunction test since paraphyllia of different types never occur in any single individuals. Therefore, paraphyllia of different types in mosses are likely to be convergent (cf. Patterson, 1982; Table 3). That is, they evolved far more than once during evolutionary history.

Table 3. Patterson's three tests on morphological characters in mosses.

Characters	Similarity test	Conjunction test	Congruence test	Relationship
1. Between types of paraphyllia	fail	pass	fail	convergence
2. Ox- and deer-horn paraphyllia	pass	pass	pass	homology
3. Reindeer- and ox-horn paraphyllia.	pass	pass	fail	parallelism
4. Filiform paraphyllia and rhizoids in *Helodium*	fail	fail	pass	two homologies
5. Filiform paraphyllia of *Climacium* and *Helodium*	pass	pass	fail	parallelism
6. Lacinate paraphyllia and leaves in *Thelia*	pass	fail	pass	homonony
7. Axillary hairs of different numbers of apical cells	pass	not testable	fail	parallelism
8. Axillary hairs of *Myurella* and *Helodium*	pass	pass	pass	homology
9. Late central strands in Hylocomiaceae	pass	pass	fail	parallelism
10. Lacking central strands in clade *Antitrichia*	pass	pass	pass	homology
11. Sporophyte in *acrothamnium* complex	pass	pass	pass	homology

Convergent evolution of paraphyllia, which lack a recent common ancestor, is more likely to be due to selection (Patterson, 1982; Brooks and McLennan, 1991). Similar vegetation (temperate forests) and habitats (moist environments) are correlated with the occurrence of paraphyllia. Nevertheless, the topography and initiation of paraphyllia remain unaltered. The design limitation on paraphyllia can be ascribed to structural constraints (Hall, 1992).

Within Hylocomiaceae two types of paraphyllia, horn-type and triangular-type, appear to be convergent. Based on the cladistic analysis (Fig. 4) triangular paraphyllia, an autapomorphy of *Orontobryum*, evolved independently from the horn-type without deriving the characters from their common ancestor. On the other hand, the description of three subtypes of horn-like paraphyllia is based on their ontogenetic sequences. Among them the homology of ox-horn (in *Loeskeobryum*) and deer-horn (in *Hylocomium*) paraphyllia is supported by similarity, conjunction, and congruence tests. Heterochrony is found between the ontogenetic transformations of the two types of paraphyllia. However, both types seem to diverge at the same time from their common ancestor; there is no basis for polarizing which type is primitive. From the developmental sequence the deer-horn type is one more step along a developmental pathway than is the ox-horn type (Fig. 1A). If the deer-horn paraphyllia was the ancestral type, ox-horn paraphyllia evolved by truncating the developmental sequence (paedomorphosis). If the ox-horn type was primitive, the deer-horn paraphyllia would evolve by extending the development of ox-horn stage (juvenile and ancestral type). Earlier fossil records of *Hylocomium* (Miller, 1984), tracing back to Miocene, favor the former hypothesis.

Another type of horn-like paraphyllia (in *Hylocomiastrum*), reindeer-horn type, appears to be homoplastic with the two above types based on the congruence test (Fig. 4, Fig. 1A).

The parallel evolution of paraphyllia is ascribed to the Bauplan, the basic structural plan (Eldredge, 1989), from their common ancestor (Wake, 1991) based on the evidence of shared ontogenetic transformations. Compared to deer-horn paraphyllia, reindeer-horn paraphyllia develop further by foliating the branches of paraphyllia (Fig. 1A). The process of heterochrony (repatterning) may play the role of internal forces, which channel the variation of ontogenetic pathway. On the other hand, similar environmental selection, such as for the same vegetation type, may be the external forces responsible for the parallel evolution of paraphyllia.

A unique type of paraphyllia with a bifurcating filiform pattern (Fig. 1E) is shared by *Climacium* and *Helodium*. Interestingly, the morphology and coloration of filiform paraphyllia resemble those of rhizoids. Ireland (1968) interprets paraphyllia in *Pleuroziopsis*, a sister group of *Climacium,* as modified rhizoids borne on the top of lamellae. Comparison of the structures (Table 4) reveals the convergent evolution of paraphyllia and rhizoids. Both filiform structures initiate from the epidermal cells of a stem or branch and are brown, which is unusual for paraphyllia. Cell walls of rhizoids are oblique and the branching pattern in rhizoids is irregular, whereas cell walls of paraphyllia are transverse and the branching pattern of paraphyllia is regularly bifurcating. In addition, the brown basal portion of early stage transforms into a clear structure. At infraspecific levels paraphyllia and rhizoids fail Patterson's similarity and conjunction tests. They appear to be two different characters (Table 3).

Table 4. Comparison of morphology of filiform paraphyllia and rhizoids in *Climacium* and *Helodium*.

	Filiform paraphyllia	Rhizoids
1. shape	filiform	filiform
2. topography	stem and branch	stem and branch
3. origin	epidermal cells	epidermal cells
4. color of basal part	brown	brown
5. composition of basal part	2-row cells	single-row cells
6. branching	regular, bifurcating	irregular
7. color of top portion	clear	brown

The parallel evolution of filiform paraphyllia in *Climacium* and *Helodium blandowii* might be ascribed to similar environmental selection, although the function of paraphyllia remains unknown. Plants of both taxa grow in wet habitats along streams (Crum and Anderson, 1981), suggesting a possible functional adaptation of paraphyllia.

"Laciniate" paraphyllia (Fig. 1C), a unique feature in *Thelia*, have laciniate and ciliate margins. Three species of the endemic genus in North America share the same ontogenetic transformations of paraphyllia with some modifications in shape. The margins of paraphyllia are highly correlated with those of leaves. For example, leaves and paraphyllia of *Thelia hirtella* (Hedw.) Sull. have dentate margins; in contrast, those in *T. lescurii* Sull. have ciliate-papillose margins. Lacinate paraphyllia are distinguished from leaves by the absence of costa. In addition, paraphyllia are usually smaller than leaves. Based on the above observations it might be hypothesized that paraphyllia and leaves in *Thelia* may be different developmental stages of the same character; in other words, paraphyllia are juvenile leaves. However, differentiated costae found in the younger leaves around stem tips suggest otherwise. Regardless, paraphyllia and leaves share a similar ontogenetic pathway. They pass both similarity and congruence tests (Fig. 4), but fail the conjunction test. They are likely to be homonomy (mass homology) (Patterson, 1982, Riedl, 1979) or iterative homology within single organisms (Roth, 1991).

The study of the relationship between paraphyllia and leaves in mosses may make little direct contribution to our understanding of phylogeny relationships of taxa. Nevertheless, knowledge of character phylogeny (Roth, 1991) and the biological basis of homology [cf. biological homology of Wagner (1989a] will enhance the understanding of morphological evolution at different hierarchical levels.

2). Homology and evolution of central strands

The conducting tissue of bryophytes with conservative morphology and structure has been well studied (Hébant, 1977). In pleurocarpous mosses (e.g., Hylocomiaceae) most taxa have a simple structure of conducting strands (Frey, 1971; Fig. 2). Functional constraints appear to be the mechanisms defining the Bauplan of conducting structure with little apparent variation throughout long periods of evolutionary time.

Heterochrony plays a critical role on the evolution of central strands in pleurocarpous mosses. A secondary loss of central strands by truncating the development (paedomorphosis) at the juvenile stage of the ancestral state (early central strands) occurs in a common ancestor of the clade of *Antitrichia* (Figs. 2 & 4). That is, the lack of central strands in this clade is a homologue supported by Paterson's tests (Table 3). In the Hylocomiaceae, *Hylocomium* and *Leptocladiella* have a secondary loss of central strands. However, a reversal of this trait (secondary gain) occurs in *Loeskeobryum,* which manifests the Bauplan for the ontogenetic pathway of central strands in this family. Parallel evolution of late central strands (Figs. 2 & 4) occurs in *Loeskeobryum* and *Hylocomiastrum* by extending the juvenile stage prior to the differentiation of central strands (hypermorphosis) without changing the adult morphology.

The differentiation of central strands seems highly correlated with the dimensions of stems or branches. The central strands, if present, transform in the branches from tips downward. In other words, central strands are not differentiated until the branches grow to a certain size (Fig. 2). The "early central strands" taxa (e.g., *Rhytidium*) appear to have blunt stem-tips. In contrast, a tapering end occurs in the stem-tip of the "late central strands" taxa (e.g., *Loeskeobryum*). The development of central strands seems to be constrained by other physical parameters of stems (e.g., the size; "developmental threshold" concept in Mueller and Wagner, 1991). Nevertheless, ontogenetic data provide only a preliminary insight into morphological evolution in mosses. To understand the biology of morphological evolution of central strands at the organismal and population levels more evidence from quantitative genetics is required.

3). Homology and evolution of axillary hairs

Axillary hairs with different number of apical cells share the same ontogenetic transformations (Fig. 3) and topography. However, nested hierarchical relationships among character states are not supported by cladistic analysis (Fig. 4). The hypothesis of homology of axillary hairs of different cell numbers does not pass the congruence test (Table 3). Nevertheless, the conservative structure and development of axillary hairs in mosses (almost all taxa) appear to be channeled or canalized (Waddington, 1957). The direction of change in a developmental sequence is limited either by extending or truncating the number of apical cells. The Bauplan of the morphology of axillary hairs in mosses, both acrocarpous (Griffin, 1990; Murray, 1988) and pleurocarpous mosses (Whittemore and Allen, 1989; Higuchi, 1985; Hedenas, 1989), is ascribed to structural constraints derived from their common

ancestor (Hall, 1992). Since axillary hairs are iterative structures, every developmental stage, which also represents the terminal stage (or character state) in the sister taxa, can be found in single individuals. Axillary hairs cannot be subject to Patterson's conjunction test.

In certain clades axillary hairs are homologous, such as two apical cells in *Hylocomiastrum* and *Neodolichomitra*, four apical cells in *Myurella* and *Helodium* (Fig. 4). Heterochrony in the development of axillary hairs is a common mode in Hylocomiaceae. Phylogenetically, 2-celled axillary hairs in *Hylocomiastrum* and *Neodolichomitra* (Fig. 3) are a derived state compared to 3-celled ones in the sister group (*Macrothamnium* complex) and the outgroups. Axillary hairs evolved from the ancestral state of three apical cells into two apical cells by truncating ontogenetic transformations. Neoteny, one of the paedomorphosis processes (Alberch *et al.*, 1979; Raff and Wray, 1989), is operating on the evolution of 2-celled axillary hairs by retaining the juvenile morphology of the ancestral state (3-celled) in adults. In contrast, the evolution of axillary hairs with four apical cells in *Myurella* and *Helodium* (Figs. 3 & 4) is a process of acceleration, one of the peramorphosis expressions, by extending the adult morphology of ancestral state (3-celled).

In conclusion, morphological characters of mosses are highly homoplastic. It has made most families including the Hylocomiaceae undiagnosable. The monophyly of the Hylocomiaceae was supported by sympodial growth-form with a reversal in genus *Orontobryum*. For better understanding the phylogeny and evolution of this family, more independent data from phenotypes, such as molecular sequences, are required.

Ontogenetic data of paraphyllia, central strands, and axillary hairs, provided insight into the character concept in Hylocomiaceae. It revealed that mere use of "presence or absence" of paraphyllia is not valid for phylogenetic reconstruction of the Hylocomiaceae. The evolution of paraphyllia of different types, having various ontogenetic pathway, in pleurocarpous mosses are convergent due to similar environmental selection. Recognizing the entire ontogenetic transformations as character and testing the homology by Patterson's three tests are informative for current study. Homoplasies (including parallelism, reversal, and convergence) are not useless to comparative biology and usually provide useful information for better understanding the mechanism of morphological evolution. A complementary methodology by looking at the homoplasies from both internalists (developmental constraints) and externalists (natural selection) perspectives provides insight into morphological evolution.

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Appendix 1. Selected herbarium specimens examined for morphological analysis
Hypothetical ingroup taxa:

Hylocomium splendens (Hedw.) B. S. G.
Canada: *Redfearn 36422* (MO); *Garten 22691* (MO).
USA: *Allen 10176* (MO); *Redfearn 36380* (MO); *Hermann 27553* (MO); *Chiang 31091, 31092, s. n.* (MO).
China: *Wu 448* (MO).
Japan: *Ochi 9053* (MO).
Taiwan: *Chuang 6449* (MO).

Hylocomiastrum pyrenaicum (Spruce) Fleisch. Ex. Broth.
Canada: *Garton 19810* (MO); *Allen 9517* (MO); *Vitt 34097* (MO).
USA: *Hermann 26922* (MO); *Voth s. n.* (MO); *Allen 10308* (MO).

H. himalayanum (Mitt.) Broth.
Japan: *Inoue 936, 487* (MO); *Schofield 51994* (MO).

H. umbratum (Hedw.) Broth.
Canada: *Schofield & Tan 60570* (MO); *Scholfield & Goward 75600* (MO).
USA: *Farlow 593* (MO); *Smith s. n.* (MO); *Chiang, s. n.* (MO).
China: *Vitt 34785* (MO).

Loeskeobryum brevirostre (Brid.) Fleisch.
Canada: *Frahm 27* (MO); *Ireland 17211* (MO).
USA: *Whitehouse 26484* (MO); *Redfearn 36387* (MO); *Fife 3058* (MO); *Chiang, s. n.* (MO).

L. cavifolium (Lac.) Fleisch.
China: *Zeng 107* (MO).
Japan: *Nakajima 688* (MO); *Koponen 77* (MO); *Mizutani 15260* (MO); *Inoue 935* (HIR).

Rhytidiopsis robusta (Hook.) Broth.
Canada: *Schofield & Tan 60773* (MO); *Vitt 33788* (MO).
USA: *Schofield 11803* (MO); *Smith 1324* (MO); *Braun s. n.* (MO); *Chiang 198, 283, 303* (MO).

Rhytidium rugosum (Hedw.) Kindb.
Canada: *Ireland 24384* (MO); *Allen 9579* (MO).
USA: *Pursell 3068* (MO); *Redfearn 28654* (MO).
China: *Redfearn 35492* (MO); *Allen 9579* (MO).
Taiwan: *Chuang 1779* (MO).

Neodolichomitra yunnanensis (Besch.) Kop.
China: *Maire s. n.* (FH); *Delavary 4636* (NY); *He 30880, 31084* (MO); *Allen 6880* (MO).

Pleurozium schreberi (Brid.) Mitt.
Canada: *Garton 21848* (MO); *Dupret 706* (MO).
USA: *Allen 9825* (MO); *Green 32* (MO); *Allen 9737* (MO); *Chiang s. n.* (MO).
China: *He 31798b* (MO); *Allen 6738* (MO); *Whittmore 3969* (MO).

Rhytidiadelphus loreus (Hedw.) Warnst.
Canada: *MacFedden s. n.* (MO); *Worley 7993* (MO); *Allen 2162* (MO).
USA: *Soukup s. n.* (MO); *Smith 1362* (MO); *Telford 4045* (MO); *Chiang s. n.* (MO); *Allen 9388* (MO).

China: *Koponen 337180* (MO).
R. squarrosus (Hedw.) Warnst.
Canada: *Ireland 15291, 16928* (MO).
USA: *Allen 10175* (MO); *Sharp 2865* (MO); *Frey 177945* (MO).
R. triquetrus (Hedw.) Warnst.
Canada: *Garton 23107* (MO); *Allen 96, 9657* (MO).
USA: *Redfearn 18559* (MO); *Mueller 17112* (MO); *Allen 10992* (MO); *Chiang s. n.* (MO).
Leptocladiella psilura (Mitt.) Fleisch.
India: *Hooker 754* (HOLOTYPE in FH; ISOTYPE in FH & NY)
Himalaya: *Bahadru 1* (NY)
Thailand: *Ogawa 67838* (NY).
China: *Higuchi 18108* (MO); *Li 85202* (MO).
L. flagellaris Norris & Kop.
New Guinea: *Norris 61619* (MO); *Sloover 42936* (MO).
Leptohymenium tenue (Hook.) Schwaegr.
Bhutan: *Griffith 738* (MO); *Higuchi 19042* (MO).
Mexico: *Arsene 7998* (FH).
Gutemala: *Steyernark 47590* (FH).
Macrothamnium macrocarpum (Reinw. & Hornsch.) M. Fleisch.
Java: *Fleischer s. n.*(FH); *Nyman 433* (MO).
China: *Handel-Mazzetti 394c* (BM).
Taiwan: *Chiang s. n.* (MO).
Hawaii: *Baldwin 138, 252* (FH).
M. javense Fleisch.
New Guinea: *Koponen 32955* (MO); *Norris 59911* (MO).
Java: *Fleischer 348, 1300* (FH); *Seifrig s. n.* (FH).
Philippines: *Copeland 827* (FH); *Robinson 6596* (FH).
M. leptohymenioides Nog.
Bhutan: *Griffith 735* (MO, NY); *Ludla* 384b (MO).
Sikkim: *Hooker 952* (FH).
Orontobryum hookeri (Mitt.) Fleisch.
Bhutan: *Hooker s. n.* (TYPE, FH); *Griffith s. n.* (NY).
Nepal: *Iwatsuki 753* (NY); *Long s. n.* (MO); *Griffith 2116* (MO); *Higuchi 16247, 17494* (HIR).

Outgroups:
Actinothuidium hookeri (Mitt.) Broth.
Bhutan: *Bartholomeu 149* (MO).
China: *Maire s. n.* (MO); *Redfearn & He 1369* (MO); *Redfearn 34948a* (MO).
Nepal: *Kanai 476* (MO).
Helodium blandowii (Web. & Mohr.) Warnst.
USA: *Vitt 35357* (MO).
Thuidium cymbifolium (Doz. & Molk.) Jaeg.
China: *He 32026* (MO).
Hylocomiopsis ovicarpa (Besch.) Card.
Japan: Takaki 182 (MO).

Thelia asprella Sull.
USA: *Allen 13398* (MO); *Brenner 27* (MO).
T. hirtella (Hedw.) Sull.
USA: *Allen 8566* (MO).
T. lescurii Sull.
USA: *Willis 126* (MO); *Nonnanmacher 91-10* (MO).
Gollania ruginosa (Mitt.) Broth.
China: *Redfearn 35045* (MO).
Ptilium crista-castrensis (Hedw.) De Not.
USA: *Chiang s. n.* (MO).
Hygrohypnum sp.
Canada: *Chiang s. n.* (MO).
Eurhynchium pulchellum (Hedw.) Jenn.
USA: *Chiang s. n.* (MO).
Anomodon attenuatus (Hedw.) Hueb.
USA: *Ikenberry s. n.* (MO).
A. rugelii (C.Muell.) Keissl.
USA: *Chiang 30992* (MO).
A. minor (Hedw.) Furnr.
USA: *Chiang 30945* (MO).
A. viticulosus (Hedw.) Hook. & Taylor
USA: *Redfearn 28432* (MO).
Haplohymenium triste (Ces. ex De Not.) Kindb.
USA: *Chiang 30974* (MO).
Leskea gracilescens Hedw.
USA: *Allen 10910* (MO).
Myurella sibrica (C.Muell.) Reim.
USA: *Allen 13333* (MO).
Climacium dendroides (Hedw.) Web. & Mohr.
USA: *Chiang 30976* (MO).
Antitrichia curtipendula (Hedw.) Brid.
USA: *Chiang s. n.* (MO).
Entodon seductrix (Hedw.) C. Muell.
USA: *Crosby s. n.* (MO).
Miehea himalayanum Ochyra
Himalayas: *Sabine & Miehea 6845* (Holotype; KRAM-B).
Lescuraea morrisonensis (Tak.) Nog. & Takaki
Taiwan: *Noguchi 16285* (Holotype; ??)

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根據形態及發育特徵重建的塔蘚科(灰蘚目)親緣

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摘　　要

本研究利用分歧分類學分析二十九個形態特徵以及鱗毛，中央束及腋生毛的發育特徵重建塔蘚科植物的親緣，有別於傳統的特徵觀念，本研究認定整個發育序列為特徵，並利用外群比較極化特徵。以 PAUP 軟體分析的結果，重建出二個等簡約的演化樹，並支持塔蘚科植物為單起源，包含了塔蘚、假蔓蘚、薄皮蘚、星塔蘚、新船葉蘚、大木蘚、薄膜蘚及圓蒴蘚等八屬，並與灰蘚科最為近緣；塔蘚科的診視特徵為具有合軸的生活型，但在圓蒴蘚則回溯成單軸型；垂枝蘚、擬垂枝蘚、赤莖蘚及扭垂枝蘚從塔蘚科中剔除，但形成一單源群垂枝蘚科。根據此一重建的親緣，同源假說藉由 Patterson 的相似性、同存性及一致性三測驗進行測試。在塔蘚科中，直立葉不具波紋以及缺乏葉狀的假鱗毛為原始共同特徵；而在科內階層，直立的孢蒴具有退化的蒴齒為同源構造（亦即來自共同的祖先）。非同源構造亦提供了解形態演化機制的訊息，本研究緣用一融合天擇學者及構造學者觀點的互補方法論，蘚類鱗毛的趨同演化歸因於環境的天擇；而輸導組織的建構則受功能限制體調節；假蔓蘚中心束的回蒴演化則說明發育的限制體限制發生過程的變異的作用；異時性藉著截斷或延長發育的序列則是在塔蘚科常見的形態演化模式。而腋生毛在成體時期保有幼體特徵存在於星塔蘚、擬塔蘚及假黃蘚或者在塔蘚、粗枝蘚及垂枝蘚延長其祖先型特徵的平行演化都可能歸因於發育的限制體。

關鍵詞：塔蘚科、特徵觀念、分歧分類學、單源、發育序列、親緣。

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